

Using parentage analysis to estimate rates of straying and homing in Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract

We used parentage analysis based on microsatellite genotypes to measure rates of homing and straying of Chinook salmon (*Oncorhynchus tshawytscha*) among five major spawning tributaries within the Wenatchee River, Washington. On the basis of analysis of 2248 natural-origin and 11594 hatchery-origin fish, we estimated that the rate of homing to natal tributaries by natural-origin fish ranged from 0% to 99% depending on the tributary. Hatchery-origin fish released in one of the five tributaries homed to that tributary at a far lower rate than the natural-origin fish (71% compared to 96%). For hatchery-released fish, stray rates based on parentage analysis were consistent with rates estimated using physical tag recoveries. Stray rates among major spawning tributaries were generally higher than stray rates of tagged fish to areas outside of the Wenatchee River watershed. Within the Wenatchee watershed, rates of straying by natural-origin fish were significantly affected by spawning tributary and by parental origin: progeny of naturally spawning hatchery-produced fish strayed at significantly higher rates than progeny whose parents were themselves of natural origin. Notably, none of the 170 offspring that were products of mating by two natural-origin fish strayed from their natal tributary. Indirect estimates of gene flow based on F_{ST} statistics were correlated with but higher than the estimates from the parentage data. Tributary-specific estimates of effective population size were also correlated with the number of spawners in each tributary.

Keywords: hatchery, homing, parentage, salmon, straying, Wenatchee River

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Introduction

Understanding patterns of dispersal and gene flow among populations is important for understanding how evolution works in natural populations and for informing conservation and population management. Dispersal rates influence meta-population structure (Hanski 1999), and rates of gene flow affect the likelihood of adaption to local conditions (Felsenstein 1976; Adkison 1995). Both of these factors in turn influence population viability and extinction risk (Stacey & Taper 1992; Kinnison & Hairston 2007). Rates of exchange of

breeding individuals among populations can be estimated in a variety of ways, including direct observation, telemetry, or mark-recapture using photo-identification (e.g. Calambokidis *et al.* 2001), physical tags or marks (e.g. Shapovalov & Taft 1954), or genetic identification (e.g. Palsboll *et al.* 1997). Gene flow can be estimated by identifying the offspring of migrants using genetic classification methods (Rannala & Mountain 1997), or by using observed frequencies of genotypes to estimate parameters in migration models (e.g. Wright 1978; Beerli & Felsenstein 2001).

Parentage analysis using genetic markers offers a potentially powerful method of estimating patterns of mating within and among populations (Jones & Ardren 2003; Garant & Kruuk 2005). Genetic information

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provides a natural 'tag' that is passed from parent to offspring, such that the breeding location of each can be directly compared, and there is a long history of such analysis in estimating pollen dispersal (Meagher 1986; Adams *et al.* 1992; Kaufman *et al.* 1998). More recently, such parentage-based tagging approaches have started to be used to study patterns of dispersal among animal populations (e.g. Randall *et al.* 2007; Waser & Hadfield 2011; Peterson *et al.* 2014).

Anadromous salmon and char (*Salmo*, *Oncorhynchus* and *Salvelinus* sp.) spawn in coastal rivers and streams throughout the Northern Hemisphere. These fish have a strong tendency to home to their natal stream, and studies estimating rates of homing and 'straying' for salmon date back to the early twentieth Century (reviewed by Quinn 2005). Most quantitative estimates of homing and straying rates for salmon have been obtained by marking or tagging juvenile fish in their natal river, and then quantifying the proportion of marked adults that return to that natal river compared to other streams (e.g. Quinn *et al.* 1991). Most estimates of homing and straying have been made for fish released from hatcheries, due to the need to tag large numbers of juvenile fish. Some studies have suggested that hatchery-origin fish stray at higher rates than natural-origin fish, but others have been equivocal (reviewed by Quinn 1993, 2005). There have also been numerous studies describing patterns of genetic variation among populations of Pacific and Atlantic salmon (e.g., Ferguson *et al.* 1995; Utter *et al.* 1995; Nielsen *et al.* 1996; King *et al.* 2001; Waples *et al.* 2004), and some of these have estimated rates of gene flow (e.g. Ford *et al.* 2004). More recently, several studies have used a combination of parentage analysis and genetic tagging to study fine-scale (within stream) patterns of dispersal within salmonid populations (e.g. Morrissey & Ferguson 2011; Vollestad *et al.* 2012; Anderson *et al.* 2013).

Release of artificially propagated organisms is common (Laikre *et al.* 2010), so understanding how artificial propagation influences dispersal or homing behaviour is an important problem for a variety of taxa. Here, we use parentage analysis to estimate rates of straying of Chinook salmon (*Oncorhynchus tshawytscha*) among several spawning tributaries in order to answer the following questions: (i) Do rates of straying and homing differ between hatchery and natural-origin salmon? (ii) For natural-origin salmon, how do factors such as parental origin, sex, age or spawning location influence the probability of straying and homing? Addressing these questions is important for understanding homing in wild populations and how artificial propagation programmes may directly or indirectly alter this behaviour.

Methods

Study population

Our study population is the spring-run (Healey 1983) Chinook salmon that spawn in the Wenatchee River, Washington. The spawning areas are in the upper Wenatchee River and four major tributaries of the Wenatchee River: the Chiwawa River, Nason Creek, Little Wenatchee River and the White River (Fig. 1). The population is listed as endangered under the US Endangered Species Act, and the recovery plan requires that four of the five major spawning areas be utilized (UCSRB 2007).

Since 1989, hatchery supplementation using broodstock captured within the watershed has been used to increase abundance, and the hatchery has produced ~50–80% of the spawners in the river each year (Ford *et al.* 2013). Here, a hatchery-origin fish refers to a fish whose parents were spawned in the hatchery, and a natural-origin fish refers to a fish whose parents spawned in the stream, regardless of their prior ancestry. The hatchery programme was founded in 1989 with collections of natural-origin fish in the Chiwawa River. Subsequently, adult fish for broodstock are captured either at a weir in the Chiwawa River near its mouth or, for marked hatchery-origin fish only, at Tumwater Dam (Fig. 1). Fish are spawned and their offspring initially reared at Eastbank Hatchery on the Columbia River (Fig. 1; WDFW 2009). Juvenile fish are transferred in September of the following year and overwinter in an acclimation pond off of the Chiwawa River 1 km upstream from the confluence with the Wenatchee River and are released in April as smolts. Prior to their release as juveniles, hatchery-origin fish are marked for subsequent identification by an adipose fin clip and/or insertion of a coded wire tag (CWT). After one to three years at sea, the fish return to spawn naturally along with natural-origin fish from the same population.

Sample collection

From 2004 to 2010, nearly all migrating spring Chinook salmon were intercepted and sampled at Tumwater Dam below the major spawning areas (Fig. 1). Each fish was sexed, scanned for passive integrated transponder (PIT) tags (fish without a PIT tag had one inserted during sampling) and coded wire tags, and the presence or absence of the adipose fin (indicating natural or hatchery origin, respectively). Tissue samples were collected from the caudal fin and stored on blotter paper (Lahood *et al.* 2008). Assignments of fish to specific tributaries were determined from PIT tag detections on the spawning grounds. Spawning ground surveys of all spawning

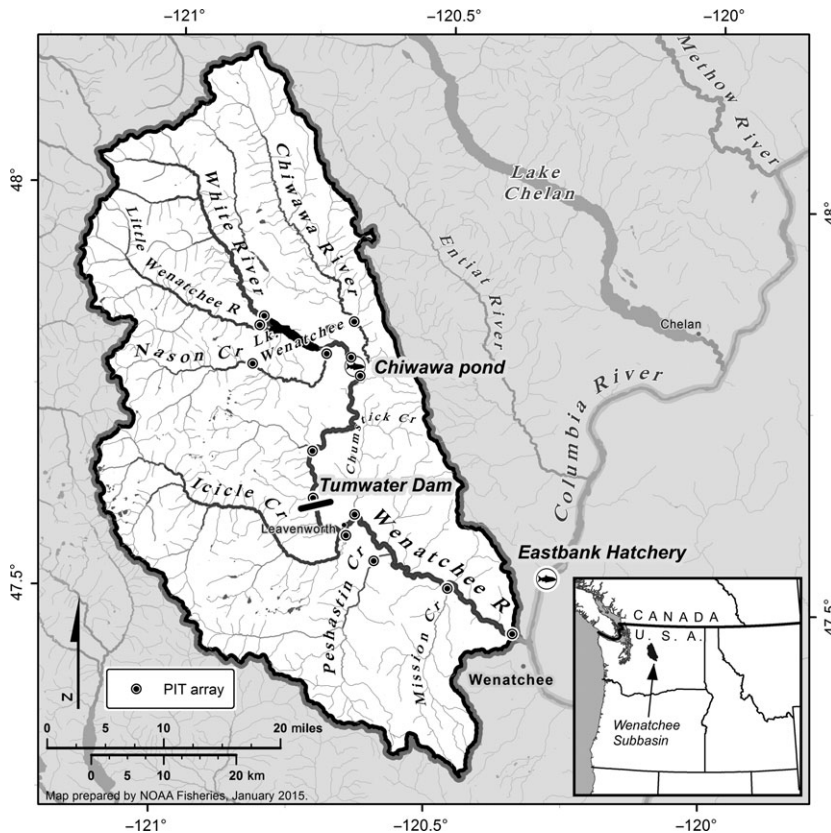


Fig. 1 Map of the study area. Major spawning tributaries within the Wenatchee Basin include the Chiwawa River, Nason Creek, White River, Little Wenatchee River and the upper Wenatchee River between the confluence of the Chiwawa River and Nason Creek. Tumwater Dam is the location where upstream migrating adults were sampled, and the Chiwawa pond is the location of hatchery smolt acclimation and release.

habitat were conducted twice a week throughout the entire spawning season (Murdoch *et al.* 2008). During these surveys, recovered carcasses and live fish associated with redds were scanned for PIT tags. For live fish, detection consisted of using an underwater antenna mounted on an extension pole. Detections on a series of continuously operating in-stream detection arrays also contributed to location information (Fig. 1). Detection efficiency of the arrays varied among streams and ranged from 10% to 77% (AM, unpublished data). For detections on arrays with no corresponding carcass or live-redd detection of the same tag, spawning tributary was assigned as the tributary containing the array of last detection. Surveys accounted for 20–24% of detections in the major spawning areas, except for the White River where they made up 90% of detections. For carcass and live-redd detections, the locations of detections were recorded using handheld GPS devices and converted to river kilometre using ARCVIEW 9.2. Detections were matched with biological data collected at Tumwater Dam using the unique PIT tag codes. All sampling activities were conducted under Endangered Species Section 10 Permit #1196.

Genetic analysis

Genomic DNA was extracted from fin clips according to the method of Lahood *et al.* (2008). All individuals

were genotyped at 15 microsatellite loci as previously reported (Ford *et al.* 2012; Table S1, Supporting information). Briefly, microsatellite loci were amplified by polymerase chain reaction (PCR), and allele sizes were electrophoretically resolved on an ABI 3100 Genetic Analyzer and scored according to the method of Winans *et al.* (2004). The approximate genotyping error rate per locus (including both mis-scoring and effects such as upper allele dropout) was determined by re-amplifying and re-scoring microsatellite loci for ~10% of individuals, and calculating the number of alleles mis-scored over the total number of alleles observed at each locus. Error rates averaged ~1% per locus. See Williamson *et al.* (2010) and Ford *et al.* (2012) for additional details.

We used parentage analysis to directly compare the spawning locations of offspring with that of their parents. Parentage assignments were conducted using the Bayesian method implemented in the computer program FRANZ (Riester *et al.* 2009). Assignments were conducted separately for each group of annual spawners and their offspring (spawning years 2004–2006; offspring years 2006–2010). Prior information incorporated into the analysis included identification of parental and offspring groups, parental sex and the number of potential parents of each sex. The latter was determined separately for males and females. For females, we assumed

that all potential parents were sampled at Tumwater Dam, and the total number of females was therefore set as the observed number. For males, we set the number of potential spawners as the number sampled at Tumwater Dam plus an additional 25%, to account for the potential presence of sexually mature parr (Larsen *et al.* 2013).

Homing and straying among spawning areas within the Wenatchee watershed

The homing rate to a spawning tributary was estimated as the proportion of progeny that returned to the same spawning tributary as their parents. The stray rate, defined as the proportion of progeny originating from one of the five major spawning tributaries that returned to a different spawning tributary, was calculated as $1 - \text{the homing rate}$. Finally, the immigration fraction was estimated as the proportion of natural spawners in a tributary whose parents spawned in a different tributary. We evaluated the effects of offspring sex, brood year, parental origin, offspring age, and parental spawning tributary on the probability of offspring straying using logistic regression ('glm' function in R (R Core Team 2012) with a binomial error distribution and a logit link function). For hatchery-origin fish released as tagged (CWT) smolts in the Chiwawa River, we also estimated the homing rate back to the Chiwawa using estimated CWT recoveries from 2004 to 2010, as a point of comparison to the parentage-based estimates.

Two spawning tributaries, the Chiwawa River and Nason Creek, had spawners distributed over 30–50 linear kilometres of stream, allowing for more detailed analysis of homing and straying. For these two tributaries, regression analysis was used to examine the relationship between maternal and offspring spawning locations.

As a comparison to the parentage analysis, patterns of genetic variation within and among the major spawning tributaries within the Wenatchee were also

explored in several ways. The proportion of total variation that was variation among locations (F_{ST}) and the fit of genotype frequencies within tributaries to Hardy–Weinberg equilibrium expectations was estimated using the method of Weir & Cockerham (1984) as implemented in the program GENEPOP (Rousset 2008). Matrices of F_{ST} estimates among spawning areas and sample years were visualized in a two-dimensional scaling plot using the 'cmdscale' function in the R statistical framework (R Core Team 2012).

The effective population size (N_e) of each major spawning area was estimated using the linkage disequilibrium method in the LDNE computer program (Waples & Do 2008). Due to small annual sample sizes for some populations (Table 1 and Table S2, Supporting information), we used all natural-origin samples associated with a spawning area from 2004 to 2010 for estimating N_e . Confidence intervals were estimated by jackknifing over loci, and sensitivity to low-frequency alleles was tested using low-frequency cut-offs ranging from 1% to 5%. We were interested in comparing immigration fractions estimated from parentage analysis with those estimated from genetic differentiation among tributaries. We used pairwise estimates of F_{ST} for all years combined to estimate the migration parameters in an n -deme migration model (Wright 1978; Slatkin & Voelm 1991). Under this model, the expected relationship between F_{ST} and the migration parameter, m , is $F_{ST} \approx 1/(4Nma + 1)$, where $a = (n/(n-1))^2$ (Slatkin & Voelm 1991). We used $n = 4$, to represent the four largest spawning areas. Estimates of $4Nm$ were then converted to estimates of immigration fraction m by dividing them by the four times the independent estimates of effective size obtained from the LDNE method.

Stray rates to areas outside of the Wenatchee River watershed

The parentage analysis was limited to areas within the Wenatchee River. To put this analysis in a broader

Table 1 Comparison of mean annual passive integrated transponder tag recoveries (2004–2010), an index of annual spawning abundance, with the estimates of effective population size obtained from the linkage disequilibrium method (Waples & Do 2008). The 95% confidence intervals are in parenthesis, along with the average proportion of the total in each spawning area

Spawning area	Annual PIT tag recoveries		Effect population size Natural-origin
	Hatchery-origin	Natural-origin	
Chiwawa River	1140 (399–1882, 0.69)	180 (75–285, 0.55)	516 (439–612, 0.41)
Little Wenatchee	50 (6–93, 0.03)	19 (8–30, 0.06)	160 (134–195, 0.13)
Nason Creek	398 (157–640, 0.24)	93 (64–122, 0.29)	421 (386–462, 0.34)
Upper Wenatchee	39 (6–73, 0.02)	3 (2–4, 0.01)	NA
White River	36 (11–61, 0.02)	31 (16–45, 0.09)	156 (139–175, 0.12)

context, we used CWT and PIT tag data to estimate rates of straying from the Wenatchee to two adjacent watersheds that are regularly surveyed for tags: the Entiat and Methow rivers (Fig. 1). All CWT release and recovery data (hatchery-origin fish only) were obtained from the Regional Marking Information System (RMIS) database (<http://www.rmipc.org>). Juvenile spring Chinook salmon were PIT-tagged at a smolt trap located near the hatchery acclimation pond on the lower Chiwawa River. Stray rates outside the Wenatchee watershed were calculated based on PIT tag detections of returning adults at hydroelectric projects on the Columbia River and numerous in-stream PIT tag arrays deployed throughout the Upper Columbia. All PIT tag detections were queried from the PTAGIS database (<http://www.ptagis.org>).

Results

Genetic variation among spawning areas within the Wenatchee watershed

We genotyped 4084 natural-origin and 23 550 hatchery-origin spring chinook that were sampled and passed above Tumwater Dam. Of these, 2248 natural-origin and 11 594 hatchery-origin fish were identified with a major natural spawning area based on PIT tag detections (Tables S2 and S3, Supporting information). A majority of the fish spawned in the Chiwawa River, with less than third spawning in Nason Creek and <10% in the White or Little Wenatchee rivers (Table 1). Based on the PIT tag detections, only 52 natural-origin fish (2.3%) were detected in more than one tributary. Of these, only 16 (0.7%) occurred during the spawning period, and no fish were actually observed to have spawned in multiple tributaries. In contrast, 13.1% of hatchery fish were detected in multiple tributaries during the spawning period.

For the sample considered as whole, allele frequencies at most loci departed statistically from random mating expectations, but departures were small (Table S1, Supporting information) and not expected to affect the parentage analysis (Riester *et al.* 2009). Averaged over all years, F_{ST} among natural-origin fish from the three primary spawning areas was significantly > 0 ($P < 0.001$) but very low, ranging from 0.0025 (Chiwawa vs. Little Wenatchee) to 0.0077 (Nason vs. White) (Table S4, Supporting information). The degree of differentiation varied over time. With the exception of 2009, samples from the White River were differentiated from the other spawning areas, as were samples from Nason Creek in 2004 and 2008 and the Little Wenatchee River in 2005 and 2006 (Fig. S1, Supporting information).

Parentage assignments

Posterior probabilities from the parentage analysis averaged 0.95 when two parents were assigned, and 0.94 when single-parent or no-parent assignments were included. Of the natural-origin progeny analysed, 70.2% were assigned to two parents, 19.3% to a female parent only, 7.1% to a male parent only, and 3.4% to neither parent. The tendency for missing natural-origin parents to be male suggests that the mature parr (which would not be included in parental samples) are contributing some matings. Some spring Chinook salmon that return late in the season when thousands of sockeye salmon and summer Chinook salmon are also returning may also not have been sampled due to constraints of handling large number of fish over the dam. As a test of sensitivity of parentage results in missing parents, the analysis was also conducted assuming 7% missing female parents in addition to the 25% missing male parents. Under this assumption, 98% of the assignments were identical to the case assuming no missing females, indicating that the results are not very sensitive to small violations of the assumption of the proportion of parents sampled.

Homing and straying rates among spawning areas within the Wenatchee watershed

For the parentage-based analysis of straying, there were a total of 10 367 comparisons of offspring and parental spawning location. Of these, 1095 were natural-origin offspring and 9272 were hatchery-origin offspring originated from smolt releases into the Chiwawa River. Immigration fractions ranged from 100% in the upper Wenatchee to 3% in the Chiwawa River (Table 2). Stray rates ranged from a high of 100% for fish spawning in the upper Wenatchee to 1.3% for fish spawning in the White River (Table 2). Stray rates between individual pairs of tributaries could be quite low. For example, only ~1% of the natural-origin fish originating from the Chiwawa River strayed to the White River, and only ~3% strayed to Nason Creek. Of the natural-origin strays, only two were full-siblings, indicating that straying was not due to unusual behaviour by a very small number of families. We also examined 645 fish collected for broodstock for the Chiwawa River hatchery programme, and all but six of these had parents originating from the Chiwawa River (four from Nason Creek and one each from the upper Wenatchee and White River).

Parental spawning location and parental origin both were significant predictors of straying, with offspring from naturally spawning hatchery-origin fish and offspring from spawners in the Little Wenatchee and Nason Creeks having a higher probability of straying

Table 2 Straying and homing of natural-origin Chinook salmon based on parentage analysis. Progeny spawning locations are in rows; parent spawning locations are in columns. The three numbers in each entry are from left to right: the raw counts, the proportion of progeny within a spawning area originating from the indicated column parental spawning area (immigration fractions; rows sum to 1), and the proportion of progeny originating from a spawning area that returned to the same or a different spawning area (homing and straying rates; columns sum to 1)

	Chiwawa River	Little Wenatchee	Nason Creek	Upper Wenatchee	White River
Chiwawa	694/0.973/0.959	2/0.003/0.050	14/0.020/0.057	3/0.004/0.500	0/0.000/0.000
Little Wenat.	5/0.104/0.007	33/0.688/0.825	8/0.167/0.033	1/0.021/0.167	1/0.021/0.013
Nason	19/0.078/0.026	1/0.004/0.025	222/0.910/0.910	2/0.008/0.333	0/0.000/0.000
Upper Wenat.	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0
White	6/0.071/0.008	4/0.048/0.100	0/0.000/0.000	0/0.000/0.000	74/0.881/0.987

Table 3 Parameter estimates from a logistic regression model evaluating factors influencing straying. Negative values indicate that a factor reduces the probability of straying compared to the 'baseline' factors (age 3, female, 2004, Chiwawa River, hatchery-origin); positive values indicate the factor increases the probability of straying compared to baseline factors. The baseline is arbitrary and does not influence the results

	Estimate	SE	P-value
(Intercept)	-1.75	0.81	0.031
Sex – male	-0.31	0.33	0.340
Age – 4	-0.53	0.59	0.374
Age – 5	-1.71	1.24	0.166
Brood year – 2005	-0.90	0.57	0.113
Brood year – 2006	-0.19	0.53	0.715
Natal river – Little Wenatchee	2.59	0.60	1.38E-05
Natal river – Nason	1.43	0.36	6.30E-05
Natal river – White	1.07	0.69	0.122
Mother origin – wild	-0.91	0.40	0.021
Father origin – wild	-1.45	0.42	0.0005

(Table 3). Notably, all natural-origin strays had at least one hatchery-origin parent; none of the 170 offspring that were the products of natural \times natural matings strayed from their natal stream (Table 4). Due to the relatively small number of fish that strayed and the consequently small number of observations in many cells, we did not attempt to estimate interaction terms in the model.

Within both the Chiwawa River and Nason Creek, maternal spawning location was a significant predictor of offspring spawning location (Fig. 2). In the Chiwawa River, the relationship was significantly weaker for naturally spawning hatchery-origin fish than for natural-origin fish (Fig. 2). In particular, the offspring of naturally spawning hatchery females that spawned in the lower half of the Chiwawa River displayed a strong tendency to return to spawn upstream of their mother's spawning location (Fig. 2).

Estimates of effective population size ranged from 156 (White River) to 516 (Chiwawa River), with the

Table 4 Origin of naturally spawning parents (hatchery or natural) whether or not their offspring strayed to a non-natal tributary

Parental spawning location	Origin		Offspring strayed?		
	Mother	Father	No	Yes	Stray rate
Chiwawa	H	H	241	15	0.06
	H	W	98	0	0.00
	W	H	89	3	0.03
	W	W	84	0	0.00
Little Wenatchee	All	All	512	18	0.03
	H	H	12	1	0.08
	H	W	13	3	0.19
	W	H	4	2	0.33
Nason	W	W	0	0	
	All	All	29	6	0.17
	H	H	54	10	0.16
	H	W	27	5	0.16
White	W	H	42	5	0.11
	W	W	73	0	0.00
	All	All	196	20	0.09
	H	H	20	2	0.09
All	H	W	17	0	0.00
	W	H	8	1	0.11
	W	W	13	0	0.00
	All	All	58	3	0.05
	H	H	327	28	0.08
	H	W	155	8	0.05
	W	H	143	11	0.07
	W	W	170	0	0.00
	All	All	795	47	0.06

White River and Little Wenatchee River areas having nonoverlapping confidence intervals with the Chiwawa River and Nason Creek areas (Table 1). Estimates were similar using different low-frequency allele cut-offs, and only the results for the 1% cut-off are reported. Estimates of immigration fraction based on the F_{ST} estimates and the four-deme migration model ranged from 4% to 35% and were positively correlated with but on average larger than the parentage-based estimates (Fig. 3).

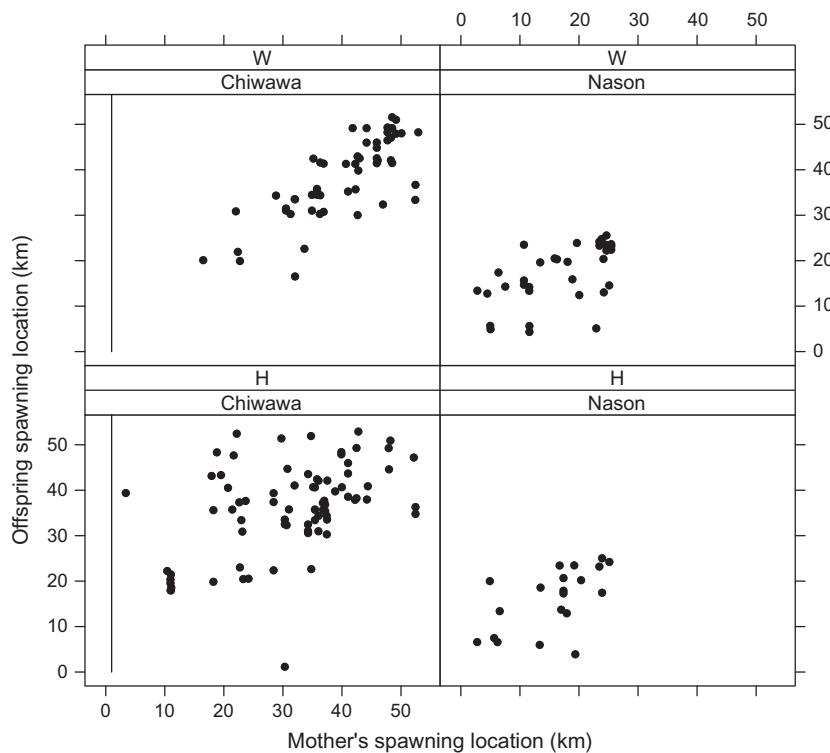


Fig. 2 Relationship of mother and offspring spawning locations in the Chiwawa River and Nason Creek for hatchery-origin (H) and natural-origin (W) mothers. The vertical black bar indicates the location of the acclimation pond and release site for hatchery-reared fish in the Chiwawa River. Starting in the upper left panel and moving counterclockwise, correlation coefficients (and P -values) were 0.77 (8.29E-12), 0.47 (6.04E-05), 0.58 (0.0072) and 0.61 (6.04E-05). The coefficients were significantly different ($P = 0.018$) between hatchery and natural mothers in the Chiwawa River, but not in Nason Creek ($P = 0.81$).

Homing rates for hatchery-origin fish released as smolts in the Chiwawa River and recovered as adults on the spawning grounds were much lower (71%; Table 5) than for fish produced by natural spawning in the Chiwawa River (96%; Table 2). The difference was due to higher rates of straying to Nason Creek: 23% for fish originating from smolt releases compared to 3% for fish originating from natural spawning. Homing rates based on CWT recoveries were similar to those obtained with parentage analysis (Table 5). Three hundred and ninety full-sib families contributed strays to Nason Creek. The mean family size of returning hatchery-origin fish was 13.5 (SD = 15.7). Within these families, an average of 24% (SD = 24%) of the offspring strayed to Nason Creek.

None of 237 PIT tags implanted in natural chinook smolts in the Chiwawa River were recovered outside of the Wenatchee watershed, suggesting a very low stray rate of these fish to other Upper Columbia watersheds. In contrast, 5% of the hatchery-origin fish tagged with CWT tags or PIT tags were recovered in other Upper Columbia watersheds (Table S5, Supporting information).

Discussion

Straying of natural- and hatchery-origin fish

Artificially propagated organisms of many taxa are commonly released in large numbers into nature for

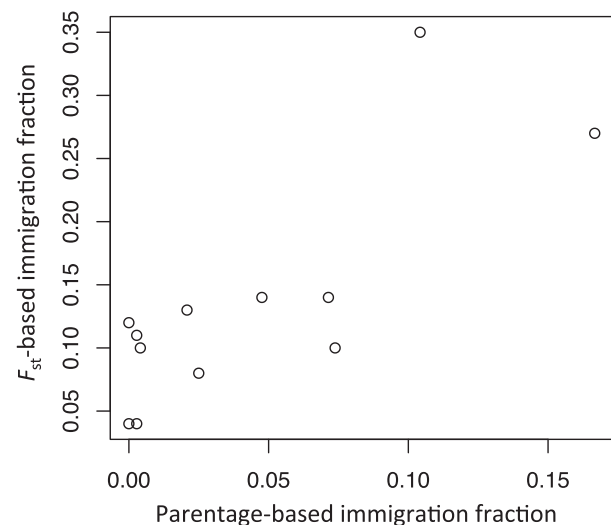


Fig. 3 Comparison of estimates of immigration fractions among spawning areas using F_{ST} - and parentage-based estimates. The correlation coefficient between the two estimates is 0.79 ($P = 0.0021$).

both conservation and utilization purposes, but the effects of such releases on the genetic structure or dispersal patterns of conspecific natural populations are rarely evaluated (Laikre *et al.* 2010). Hatchery-propagated salmonids are an exception, having been the focus of considerable research on genetic interactions with natural populations (e.g. Ryman 1991; Waples

Table 5 Number and proportion by return location within the Wenatchee River watershed of adult hatchery salmon that were released as smolts within the Chiwawa River (return years 2004–2010) calculated using coded wire tag (CWT) recoveries and parentage analysis

Receiving tributary	CWT recoveries		Parentage analysis	
	<i>n</i>	Proportion	<i>n</i>	Proportion
Chiwawa	4430	0.60	6579	0.71
Little Wenatchee	250	0.03	225	0.02
Nason	1757	0.24	2161	0.23
Upper Wenatchee/ Chiwaukum	720	0.10	136	0.01
White	244	0.03	131	0.01

1991; Araki *et al.* 2007). However, relatively little is known about differences in homing and straying between hatchery and natural salmon, largely due to the difficulties of estimating rates of homing in natural populations (Quinn 2005).

Overall, we found markedly higher rates of straying by hatchery-origin Chinook salmon released into the Chiwawa River compared to their natural-origin counterparts originating from the same stream (Tables 2 and 5). Within the Wenatchee Basin, this difference was due entirely to high rates of hatchery-origin fish straying to one other tributary – Nason Creek. The mouth of Nason Creek is only 12 stream km from the hatchery acclimation site, and this high rate of straying is likely a consequence of incomplete imprinting by the hatchery-origin fish. In particular, the practice of offsite hatchery rearing, as occurs in the Chiwawa hatchery programme, has been previously shown to result in relatively high rates of straying (e.g. Candy & Beacham 2000), possibly due to disruption of migratory-dependent imprinting mechanisms (Dittman & Quinn 1996). Within the Chiwawa River, fish released as smolts tended to stray far upstream from the location of their release site (Fig. 2), consistent with results from the nearby Yakima River (Dittman *et al.* 2010), and also strayed at relatively high rates to areas outside of the Wenatchee Basin altogether (Table S5, Supporting information). These results support some previous observations that hatchery-reared salmon stray at higher rates than natural salmon in the same streams (Labelle 1992) and suggest that altered dispersal patterns by artificially propagated organisms are an important factor to consider when evaluating similar programmes for other taxa.

The tendency for artificially propagated fish to stray at higher rates than natural-origin fish was also observed in their natural-origin progeny. Parental origin was a significant factor influencing the probability of straying (Table 3), and indeed, every natural-origin fish

we identified that strayed to a non-natal tributary had at least one naturally spawning hatchery-origin fish as a parent (Table 4). Within the Chiwawa River, the progeny of naturally spawning hatchery-origin fish also spawned further from their mother's spawning location than did those of natural-origin mothers (Fig. 2). These results suggest that the effects of altered dispersal behaviour by artificially propagated organisms may not be limited to the generation of release, but could continue to be mediated through their natural-origin progeny.

There are several potential reasons why parental origin might influence the homing tendencies of their progeny. For example, hatchery-origin fish may tend to return to spawn in poorer habitat than natural-origin fish; therefore, their progeny may tend to stray more as they seek out higher quality habitat upon their return. The upper Wenatchee area and the lower sections of the Chiwawa River, for example, are dominated by hatchery-origin fish at relatively high spawning densities, and these areas are considered to be relatively poor habitat. The higher stray rates of the natural-origin progeny of hatchery-origin fish may therefore in part be due simply to the spawning location of their parents.

However, parental spawning location does not appear to be the entire explanation. Differences in spawning location between hatchery- and natural-origin fish within a tributary are only pronounced in the Chiwawa River, for example, but the higher homing fidelity of the progeny of natural-origin fish was seen throughout the basin. Similarly, within the Chiwawa River, the progeny of natural-origin spawners displayed high homing fidelity regardless of spawning location. If fish spawning in the lower Chiwawa River simply tend to stray more due to seeking higher quality habitat, one would expect to also see this occur in the progeny of natural-origin fish.

Another possible explanation for increased straying of progeny of naturally spawning hatchery-origin fish is heritable effects due to hatchery rearing. High levels of gene flow between the hatchery and natural parts of the population make it unlikely that substantial genetic differences could accumulate between the hatchery and natural-origin fish. However, recent studies, particularly in mammals, have demonstrated that epigenetic phenomena that control gene expression, such as patterns of DNA methylation, are influenced by the environment during early development and in some cases can be passed from one generation to the next (reviewed by Matthews & Phillips 2010; Hochberg *et al.* 2011; Jonsson & Jonsson 2014). In a recent review, Li & Leatherland (2013) concluded that hatchery rearing might be expected to have an influence on epigenetic programming, particularly of genes related to endocrine

processes. Such processes are known to be critical to juvenile imprinting in salmon, and altered hormone profiles have been suggested to lead to increased straying of hatchery-origin fish (reviewed by Keefer & Caudill 2014).

One study that explicitly tested for large genomewide differences in DNA methylation between hatchery and wild steelhead (*O. mykiss*) as a cause for heritable fitness differences did not find such differences, but the authors noted that their results do not preclude differences in methylation at a smaller number of specific genes or for differences in other types of epigenetic programming (Blouin *et al.* 2010). Our results suggest that epigenetic changes in hatchery-origin fish that are transferred to their natural-origin progeny are worth investigating as a potential cause of differences in homing tendency. If propagation of organisms in artificial environments leads to rapid changes in the epigenome, this would clearly have profound implications for the risks associated with the release of such organisms.

In addition to parental origin, the other major factor influencing the probability of straying by natural-origin fish was their natal tributary (Table 3). The propensity to stray varied greatly among tributaries, with natural spawners in the Little Wenatchee River and Nason Creek producing progeny that strayed at significantly higher rates (17.5% and 9%, respectively) than those from the Chiwawa and White rivers (4.1% and 1.3%, respectively). The small number of natural-origin fish produced from the upper Wenatchee main stem area all strayed to other tributaries (Table 2).

At this point we can only speculate on the causes of these differences among tributaries, but there are some suggestive patterns. Tributaries separated by Lake Wenatchee (Fig. 1) had lower rates of straying between them than tributaries not separated by the lake. Lake Wenatchee may act as a barrier to straying, or fish originating from areas above or below Lake Wenatchee may be strongly imprinted to these areas. Considering the areas above and below Lake Wenatchee separately, there was also a pattern in which straying was higher in the direction of the larger populations: Nason to Chiwawa, and Little Wenatchee to White. Higher stray rates from less abundant spawning areas might be due to poorer habitat quality in those areas (Dittman *et al.* 2010; Cram *et al.* 2013) or might reflect a tendency for fish to be attracted to larger concentrations of their conspecifics (reviewed by Keefer & Caudill 2014).

We did not explicitly test habitat quality as a cofactor influencing probability of straying, but our results suggest that fish originating from low-quality habitat may stray at higher rates. The upper Wenatchee spawning area is one of the most degraded areas within the

Wenatchee watershed (Honea *et al.* 2009), and the fact no fish originating from this area returned there suggests that even if fish imprint there, they may seek out higher quality habitat when they return as adults. Similarly, habitat quality is more degraded in the lower sections of the Chiwawa River than in the upper sections (UCSRB 2007), so the higher stray rates of fish from the lower river might be due to fish seeking out better habitat than their natal habitat. This phenomenon has been seen for hatchery salmon in the nearby Yakima River population (Cram *et al.* 2013); here, this phenomenon may be occurring in the progeny of naturally spawning hatchery-origin fish.

Patterns of genetic variation and effective population size

Effective rates of gene flow estimated from a simple F_{ST} -based model were correlated with the rates estimated using parentage analyses (Fig. 3). This finding is somewhat surprising, given the large numbers of hatchery-origin fish spawning in most tributaries, which contribute to high rates of gene flow throughout the basin. The F_{ST} -based estimates of gene flow among tributaries were in fact higher than the immigration fractions estimated from parentage analysis, suggesting that gene flow from hatchery-origin fish has reduced the degree of genetic differentiation among these tributaries compared to what it would be naturally.

On the other hand, estimates of effective size based on patterns of linkage disequilibrium in samples of natural-origin fish were proportionally similar to annual indices of spawning abundance in the same streams (Table 1). This result indicates that, even though groups of fish in different spawning tributaries are connected by ongoing straying, the estimates of effective size were sensitive to local deme size within a spawning tributary rather than the overall meta-population size. Waples & England (2011) explored this phenomenon using computer simulations and found that estimates of effective size based on linkage disequilibrium reflected the local deme size when immigration fractions were <5–10%, and our results appear consistent with this finding. Estimates of N_e based on linkage disequilibrium are known to be subject to bias from factors such as null alleles (Sved *et al.* 2013) and violation of demographic assumptions (Waples *et al.* 2014). In addition, ongoing gene flow from hatchery-origin fish may influence the effective size estimates, as appeared to also be the case with the F_{ST} estimates discussed above. Our estimates may therefore be biased to an unknown degree, but appear to be providing consistent information on the relative size of these spawning groups.

Management implications

Our results have implications for the use of hatcheries to supplement salmon populations, and potentially for the release of propagated organisms more broadly. The current Chiwawa River hatchery programme, for example, appears to be leading to much higher than natural rates of straying of hatchery-origin fish from the Chiwawa River into Nason Creek. Modifications to the programme to reduce this straying might therefore be important for restoring more natural patterns of dispersal within the Wenatchee Basin. The Chiwawa River hatchery programme is typical of many such programmes throughout the North Pacific, and our results suggest that such programmes could have widespread impacts on patterns of straying and homing. Most importantly, if the reduced homing tendencies of the progeny of naturally spawning hatchery-origin fish are due to genetic or epigenetic effects caused by hatchery rearing, this would be cause for considerable concern as it would mean that the diversity of this population is being fundamentally and perhaps permanently altered by the hatchery programme.

Our results also have implications for prioritizing habitat restoration. In particular, if poor habitat contributes to an increase in straying, then habitat restoration projects targeting spawning habitat may reduce observed stray rates. The 100% stray rate of the small number of fish produced by naturally spawning hatchery-origin fish in the upper Wenatchee River, for example, suggests spawning habitat in this historical major spawning area might be completely unsuitable and extensive restoration may be required to make this a productive spawning area. More broadly, our results strongly support previous recommendations that habitat suitability is a critical consideration for the success of captive re-introduction efforts in many different taxa (e.g. Hirzel *et al.* 2004; Wronski 2010; White *et al.* 2012).

Long-distance migrations between breeding and feeding areas are a characteristic of a diversity of vertebrate and invertebrate taxa (Alerstam *et al.* 2003). Captive breeding followed by release into the wild is also a common strategy for the conservation of threatened migratory species (Champagnon *et al.* 2012), including birds (Villers *et al.* 2010), reptiles (Frazer 1992) and fish (Lorenzen *et al.* 2010). The mechanisms for navigation and homing vary across taxa, including both innate and learned behaviours as well as imprinting (Baker 1978; Alerstam *et al.* 2003; Alerstam 2006). Our results add to a growing body of science indicating that captive breeding has the potential to disrupt the ontogeny of migratory behaviour in unexpected ways. For example, like salmon, sea turtles also make ocean migrations of thousands of kilometres to ocean feeding grounds, followed

by homing to their natal beaches (Luschi *et al.* 2003). Recently, Fuxjager *et al.* (2014) demonstrated that the magnetic environment juvenile loggerhead sea turtles (*Caretta caretta*) experience during incubation significantly influences their subsequent homing ability, and suggested that propagation techniques (e.g. protection by metallic cages during incubation) might influence subsequent migratory behaviour. Such similar results across diverse taxa suggest that it is important to evaluate the effects of even relatively brief periods of captive propagation and juvenile rearing on subsequent migratory behaviour.

In the specific case of Wenatchee River Chinook salmon, the conservation implications of elevated rates of straying by hatchery-origin fish and their natural-origin progeny vary depending on several factors not addressed by this study. If environmental differences among tributaries create selection pressures for local adaptation (Taylor 1991; Fraser *et al.* 2011; Peterson *et al.* 2014), then elevated rates of straying would be expected to erode such adaptations and lead to lower overall productivity of the population. On the other hand, straying has been shown to be effective at reducing rates of extirpation (Hill *et al.* 2002), so elevated rates of straying within an endangered population may be beneficial by maintaining the density of spawners above critically low levels. Similarly, if hatchery-origin fish or their natural offspring tend to stray at higher rates because they are seeking out higher quality habitat than their natal areas, this might be an adaptive strategy that increases the effectiveness of hatchery supplementation. The key piece of information distinguishing these alternatives is the degree of local selection pressure, so studying the degree to which selection pressures differ among and within tributaries is a high priority for designing effective management strategies for supplementation.

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Data accessibility

Microsatellite genotypes, phenotypic data, spawning locations and inferred parent/offspring relationships: DRYAD entry doi:10.5061/dryad.hv431.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Multi-dimensional scaling plot of pairwise F_{ST} estimates by return year and four major spawning areas (N = Nason, C = Chiwawa, W = White, L = Little Wenatchee).

Table S1 Microsatellite loci used for genetic analysis and a summary of genetic diversity statistics.

Table S2 PIT tag recovery location for each spawning area and year, natural-origin fish.

Table S3 PIT tag recovery location for each spawning area and year, hatchery-origin fish.

Table S4 Estimates of F_{ST} among the three major spawning areas for all years combined.

Table S5 Number and proportion of adult natural and hatchery offspring originally released within the Chiwawa River (return years 2008–2012) and returning to other Upper Columbia River watersheds calculated using coded wire tag (CWT) recoveries and PIT tag detections.